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UKIO URATA

HAWAII AGRICULTURAL EXPERIMENT STATION, UNIVERSITY OF HAWAII

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THE AUTHOR

Mr. Ukio Urata received the degree of Master of Science from the University of Hawaii in June 1953. The subject matter of this technical bulletin is from the thesis of Mr. Urata, which was submitted to the Graduate School of the University of Hawaii in partial fulfillment of the requirements for the degree.

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CONTENTS

POLLINATION REQUIREMENTS OF MACADAMIA

Macadamia ternifolia, Muell., a tree native to Queensland, Australia, is becoming increasingly important as an orchard crop in Hawaii. It has two recognized botanical varieties. These are *Macadamia ternifolia* F. v. M. and *Macadamia* F. v. M. var. *integrifolia* (Maiden and Betche) Maiden. *Macadamia ternifolia* F. v. M. is the rough-shelled macadamia, and the *Macadamia* F. v. M. var. *integrifolia* is the smooth-shelled macadamia. Since most of the work herein described was done on the smooth-shelled variety, the common name "macadamia" will be used to describe that variety.

Most of the bearing, local-seedling orchards derive from two introductions of the smooth-shelled type. The first of these was made at Kukuihaele in the 1880's by W. H. Purvis, and the second was made on Wyllie Street, Honolulu, in 1892, by E. W. and R. A. Jordan. Pope (*19*) stated that there were still six plants of this introduction left standing at the home of E. W. Jordan. According to a personal communication received from Ralph Moltzau, formerly with this Station, most of the rough-shelled plantings in Hawaii derive from a planting made in 1900 by the Territorial Board of Agriculture and Forestry. Remnants of this original planting still exist at the former U. S. Department of Agriculture Station at Tantalus in Honolulu.

Moltzau stated that the Nutridge Orchard, containing seedling trees from which most of the named horticultural varieties are derived, came from the Jordan introduction. According to a personal communication received from Leon Thevenin, agriculturist at the Honokaa Sugar Company, the Honokaa Orchard, which is the largest seedling orchard in Hawaii, is derived mainly from a tree of the Purvis introduction and from a tree which stood on the grounds of the St. Louis College at its former location on River Street in Honolulu.

In 1936, selections were made by the Hawaii Agricultural Experiment Station from the seedling population scattered over the Territory. This population was estimated in 1935 to consist of 60,000 trees on 800 acres. Subsequently, according to Storey (*23*), five varieties were named. On further trial, according to R. A. Hamilton *et al.* (*10*), two new varieties were named. Thus, there are currently seven varieties recommended by this Station.

The newer orchard and backyard plantings of smooth-shelled macadamia are predominantly grafted trees of these and other varieties. When clonally propagated plants are set out in orchards, it becomes necessary to determine whether the plants are self-compatible, and if not, to introduce adequate pollenizers. In the mixed seedling orchards, which until quite recently have made up the bulk of macadamia plantings, no evidence of pollination difficulty was noted. Furthermore, many isolated trees are found to produce an adequate fruit set.

The purpose of this study has been to: (1) Study the floral morphology of macadamia with reference to pollination, (2) determine whether the commercial varieties are self-fertile or self-sterile, (3) seek suitable pollenizers if self-sterility is found, and (4) determine the role of pollen vectors.

REVIEW OF LITERATURE

East (*5*) in his survey of self-sterility in the flowering plants, mentioned *Macadamia ternifolia* and *Grevillea robusta* as being self-fertile. Of the other Proteaceae, A. G. Hamilton (*9*) reported *Banksia serrata* and several other Australasian species to be self-sterile. Lawson (*16*), Ballantine (*1*) and A. G. Hamilton (*9*) all agreed on the low fruit set of the Proteaceae in comparison with the numerous flowers produced. Lawson attributed this sterility, together with the wide variability of many species, to species hybridity. He based his opinion on the hybridity of the Proteaceae largely on an examination of pollen grains of the family. He mentioned that the pollen of *G. robusta* is 90 percent sterile. This was doubted by Brough (*3*). It may be noted, in passing, that a *G. robusta* tree in Hawaii was found by the author to have over 95 percent fertile pollen, also that pollen grains on a 10 percent sucrose-agar solution gave very good germination.

Scott-Elliott (*21*) reported that many South African species of Proteaceae are primarily bird-pollinated. This view was supported by A. G. Hamilton (*9*) and Brough (*3*) with reference to several Australasian species. All three writers agreed that numerous insect visitors are present, but Brough (*3*), working with *G. robusta,* mentioned that these insects are probably not responsible for cross-pollination, because of the length of the flower styles. He stated that in some species of smaller-flowered Proteaceae insects can probably effect pollination.

PLANT MATERIALS

The macadamia trees used in this study are located mostly at the Nutridge Orchard of the Hawaii Macadamia Nut Company and at the Waipahu Orchard of the Oahu Sugar Company. The Nutridge Orchard is almost entirely a seedling orchard, and six of the seven varieties named by the Hawaii Agricultural Experiment Station originated there. The Waipahu Orchard is a planting of grafted trees from early selections. In both orchards, the predominant type is the smooth-shelled macadamia.

A few experiments were carried out on four isolated trees in Honolulu.

FLORAL MORPHOLOGY AND BEHAVIOR

The macadamia flower is perfect, with one anther attached by a short filament to each of four sepals. The bud is tubular, with an enlarged cap, and is borne on a pendent raceme having from 100 to 300 flowers. The flowers occur in pairs in the axils of minute bracts. The epidermis of the ovary and the lower style is densely pubescent. The upper style is glabrous.

The style is slender and tipped with an extremely small stigmatic surface, which is lined with papillae. The stigma forms a continuation of the ventral furrow of the style; and, consequently, extends a short distance below the style tip on the ventral side of the style (figure 1). Pollen-tube conducting tissue extends from the stigma to the ovary. The conducting tissue is most massive in the club-shaped tip of the style, and the cells which make it up are glandular in appearance. Below this region, the cells of the conducting tissue after anthesis are elongated and fibrillar in appearance. The majority of the cells surrounding the conducting tissue are heavily charged with tannin.

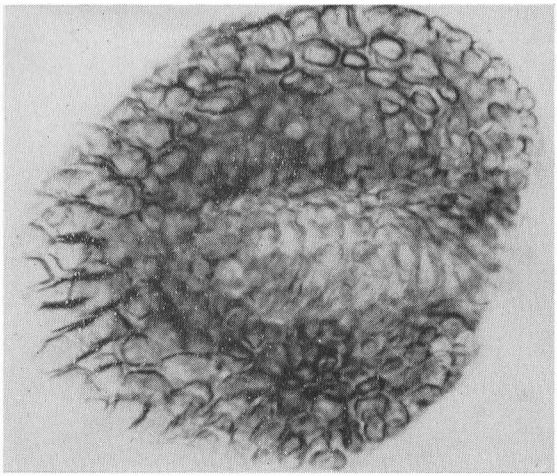

FIGURE 1. Cross section of the extreme tip of the style. The light central area is the stigmatic surface. Note that the stigmatic surface is asymmetrically placed. (× 250)

ANTHESIS

The young buds are green and usually become creamy white from 3 to 4 days before anthesis, although in some varieties, like 548 and 246, the caps remain green almost to anthesis. About 6 to 7 days before anthesis, the styles begin to elongate and bend. Finally, about 3 days later, they push through the abaxial suture between two sepals. The anthers begin to discharge the pollen 1 to 2 days before anthesis. The elongating style exerts a zipper-like pressure against the interlocking cells of the sepal suture, further enlarging the slit. One to two hours before anthesis, the sepals begin to separate at the tip and curl back, exposing the anthers. The anthers are closed over the tip of the style. After the sepals have completely recurved, the anthers begin to separate from the style, leaving the pollen masses on the style tip. Within 2 to 5 minutes, they pull entirely clear of the style tip. After this occurs, within 5 to 10 minutes the style breaks through the last unopened portion of the abaxial suture and springs free.

ANTHER DEHISCENCE

The stages of anther dehiscence and the resulting pollen deposition are shown in figures 2 to 5, which are cross-sectional views at the level of the stylar knob. The four sections shown in these four figures are photomicrographs of unopened buds. The whole process here described occurs prior to anthesis. Figure 2 shows a flower during meiosis, which occurs about 2 to 3 weeks before anthesis. These pollen-mother cells are distributed in 16 anther locules, which are served by a vascular trace in each of four anthers. The eight inner anther locules are pressed against the outer walls of the stylar knob and cause indentations at the points of contact. In figure 3, the walls between the inner and outer anther locules are disintegrating. The tapetal layers are almost completely

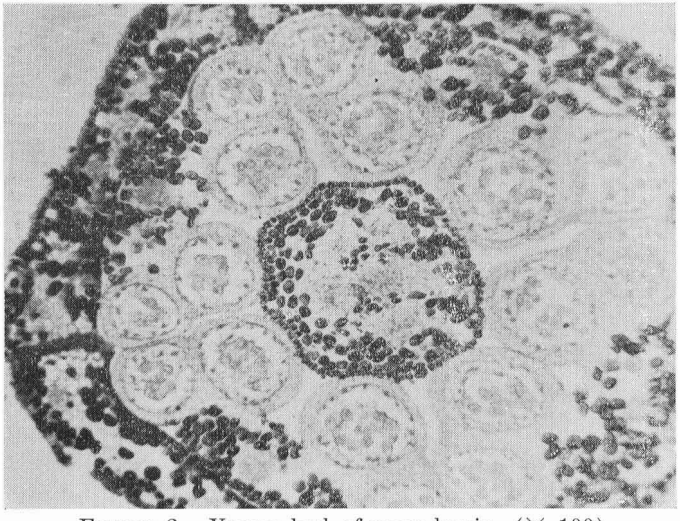

FIGURE 2. Young bud of macadamia. (× 100)

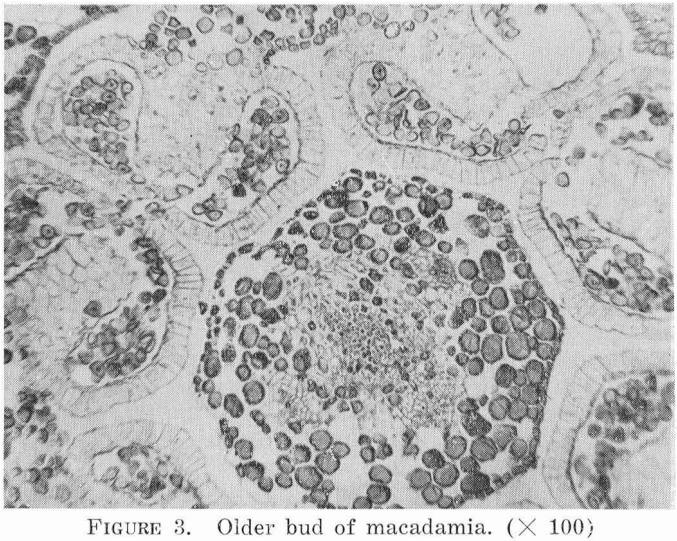

FIGURE 3. Older bud of macadamia. (× 100)

gone, and the walls of the outer anther locules have been pulled free of the stylar wall. The pollen-tube conducting tissue in the center of the style is clearly visible at this stage. So are three of the five vascular bundles, which, according to Kausik (*12*), terminate in the stylar knob. The conducting tissue is asymmetrically placed in the style, being nearest to the ventral face of the octagonal stylar knob. The heavy tannin deposits in the cells surrounding the conducting tissue are shown in all four of these photomicrographs.

In figure 4, the walls between the inner and outer anther locules are almost completely gone. The stylar walls have straightened out almost completely

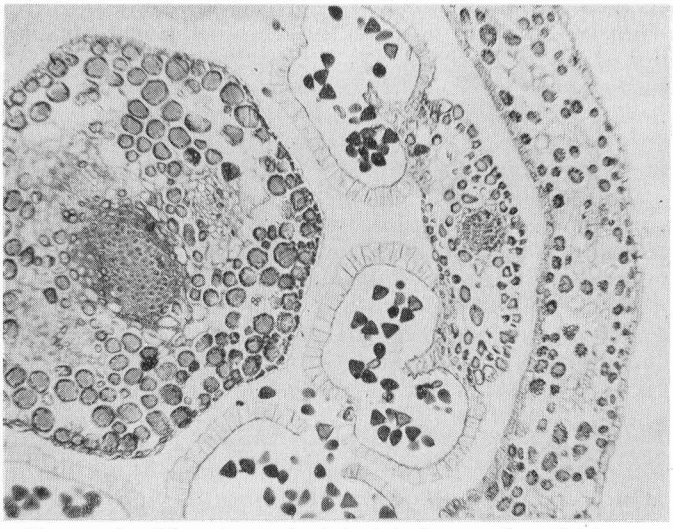

FIGURE 4. Macadamia bud just before anther dehiscence. Note the central conducting tissue in the style. (× 100)

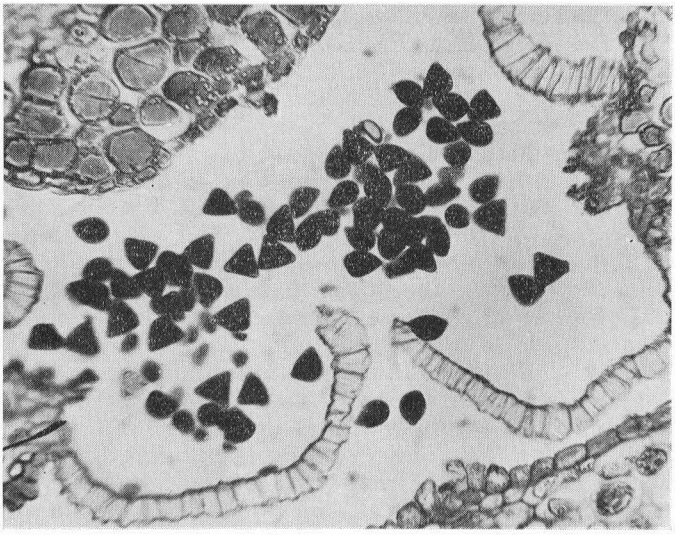

FIGURE 5. Macadamia flower at dehiscence. Note that pollen clump is made up of halves from two adjacent locules. (×200)

except on the ventral face. The origin of the four pollen clumps which occur on the style tips of newly opened flowers of macadamia is clearly seen in figures 4 and 5. They are composed of the contents of four anther locules together with the locule pairs from two adjacent anthers. From figure 3 it can be seen that each pollen clump is deposited over two adjacent faces of the octagonal stylar knob and their included angle.

In figure 5, the last stage of anther dehiscence is seen, where the endothecial anther walls of two adjacent inner locules have curled back in the process of the deposition of the pollen clump.

After anthesis, four distinct pollen masses are seen on the tip of the style. There is a small, diamond-shaped cleavage between pollen masses at the extreme tip of the style, but these pollen masses rise above the stigmatic surfaces so that the slightest disturbance would throw the pollen grains onto the stigmatic surface. It is also probable that the pollen grains are deposited on some part of the stigma at anthesis or sometime soon afterward. At any rate, in variety 404, flowers collected 48 hours after anthesis, in which the pollen clumps were intact, were found to have a majority of flowers with germinated pollen grains on the stigma. In this case, the flowers were unbagged. In other varieties, with bagged but otherwise untreated flowers, the majority of flowers were found to have germinated pollen grains. Thus, it is apparent that almost certain self-pollination is provided for in macadamia by the mechanism of anthesis.

ORDER OF FLOWERING

The racemes normally flower basipetally with adequate light, but in a shaded location they may bloom acropetally, from the center or from both ends. Two distinct orders of flower opening can be observed. In the first, most of the flowers bloom during a single day; in the second, 4 to 5 days are required. The second type of flowering results in racemes with a stratified appearance, the upper portion having flowers with sepals in the process of abscising, the middle having flowers in bloom, and the lower portion having unopened buds. At Waipahu, varieties 538, 37-6, 37-4, and 404 have the latter method.

The sepals usually remain on the flower from 2 to 3 days. After the sepals fall, the flowers with bare styles remain on the racemes from 6 to 9 days. Within 10 to 15 days after anthesis, most of the flowers have fallen. Those which remain have enlarged ovaries. This stage is designated as the "initial set". Most of the fruits of the initial set are fertilized. This was determined by paraffin sections made of young fruit at 15 days after anthesis. In most cases, these showed initiation of the endosperm.

The young fruits undergo a continual drop until about 45 to 60 days after anthesis. Those remaining become comparatively well established with the lignification of the rachis, although dropping may occur at any time up to maturity. Many of the young fruits which are lost during this early drop turn yellow before falling. At the end of the 25- to 30-day period, the pedicels of some varieties become suffused with anthocyanin. At this stage, the pedicels are still rather slender. The color becomes less noticeable as the pedicel thickens. Within a month, it disappears as the pedicel and the rachis become lignified. Lignification normally starts at the base of the rachis and at the pedicel nodes, then it extends downward over the rachis and pedicel. The lignified rachis is a semipermanent structure and lasts several years after the fall of the fruits. The diameter of the lignified rachis apparently depends on the fruit set, a raceme with a heavy cluster being several times larger in diameter than one with a single fruit.

TIME OF ANTHESIS

Macadamia, under Hawaiian conditions, is a daytime bloomer. From about 7:00 A.M. to 8:00 A.M. in the summer months, and somewhat later in the spring

and winter months, flowers with slightly separated sepal lips may be found.

Immediately after blooming, and for from 1 to 2 hours after, the style of the macadamia flower exhibits a characteristic double bend (figure 6) with one bend immediately under the terminal knob and another at the midpoint of the style. The bend under the terminal knob disappears within this 1– to 2–hour period. In the following 12 hours, the rest of the style straightens out considerably, although the middle bend never completely disappears.

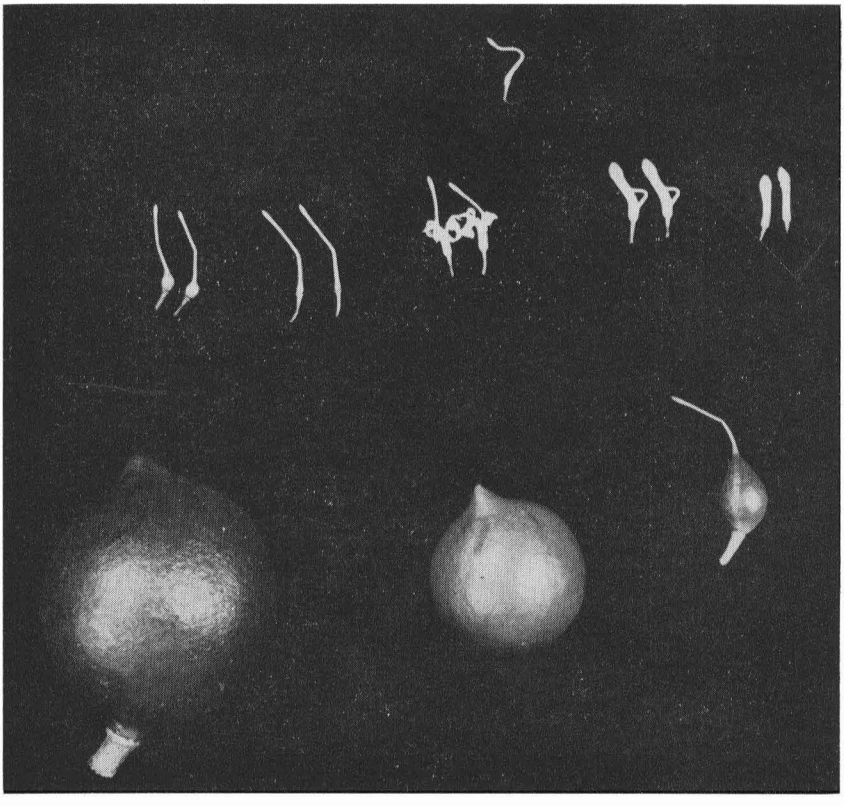

FIGURE 6. Relative sizes of buds, flowers, and fruits at various stages of development. *Top:* flower immediately after anthesis, with sepals removed, showing the double bend. *Middle, right to left:* bud at 4 to 5 days before anthesis; but 2 to 3 days before anthesis; flower, about 12 hours after anthesis; styles after sepals have fallen, 6 days after anthesis; fruits at initial set, 14 days after anthesis. *Bottom, right to left:* fruit 35 days after anthesis; fruit 60 days after anthesis, with cotyledons almost complete; fruit at maturity.

When open flowers are examined in the early morning hours, many flowers with terminal stylar pollen clumps are found, but there are no styles with the double-bend. Large numbers of double-bend flowers are observed afternoon hours. Anthesis on sunny days apparently reaches its peak after midafternoon.

POLLEN GRAINS

MORPHOLOGY

Kausik (*12*) stated that the pollen grains of *M. ternifolia* F. v. M. are tetrahedral, with the germ pores at each of the corners. Of the other proteads, Brough (*3*) reported tetrahedral pollen grains in *Grevillea robusta,* and Ballantine (*1*) reported the pollen grains of *Protea lepidocarpon* as tetragonal. Edgeworth (*6*) reported that all of the genera of proteads examined by him were trigonous, except for *Banksia* spp., which had only two germ lobes. Wodehouse (*24*) reported *Lomatia* spp. to have triangular three-lobed pollen grains, and several *Banksia* spp. to have two-lobed pollen grains.

The macadamia pollen grain, according to the writer's observations, is normally triangular in outline when viewed from the top or the bottom. Both smooth-shelled and rough-shelled types were found to have three germ lobes (figure 7). In these observations, the pollen grains were stained in acetocarmine, with a surplus of stain, and placed under the coverslip. A current was then produced in the fluid by drawing out part of the excess stain with a piece of blotting paper. This caused the pollen grains to rotate, and all sides of a single pollen grain could be examined.

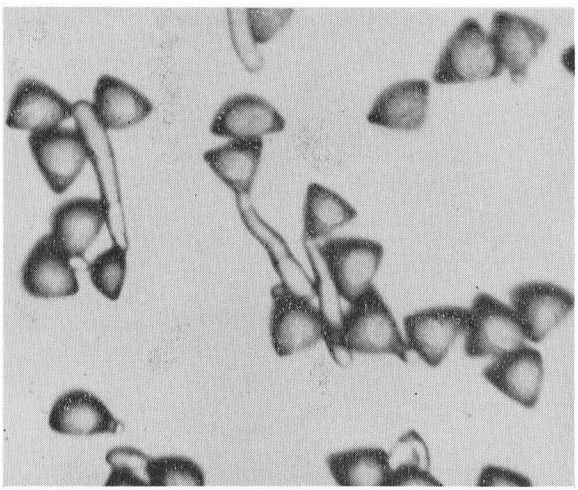

FIGURE 7. Unstained macadamia pollen grains 5 hours after sowing on cellophane-sucrose solution. Note initial callose plugs in the larger tubes.

The pollen grains, when dry, measure about 25 to 30 microns from base to apex. Side view, the pollen grain is convex on one surface; slightly concave on the other. The convex side forms the outer surface of the pollen tetrad.

The germ lobes appear on the relatively narrow edge formed by the junction of the two triangular surfaces. This became clear on examination of the polyploid variety Y–279, and two bud sports with aberrant pollen grains, since these had pollen grains which had more than three germ lobes. The macadamia chromosome number is normally n = 14. Polyploid variety Y–279 was n = 28.

POLLEN VIABILITY

Pollen viability was determined in some varieties by staining the mature pollen grains in alcohol–IKI solution or in acetocarmine. The unfilled grains were easily detected by their vocuolated appearance and their smaller size. In the named varieties treated, filled and presumably viable pollen grains were in no case less than 96 percent (table 1).

In buds collected 4 to 5 days before anthesis, both the vegetative and generative nuclei could be demonstrated in the pollen grain simply by staining in acetocarmine. This could be done in most, if not all, of the filled pollen grains. In pollen grains collected at anthesis, however, it was necessary to overstain the pollen grains with acetocarmine. This was done by letting the stain evaporate almost to dryness, then destaining with 10 percent chloral hydrate, according to the procedure suggested by Maheshwari and Wulff (*18*). The generative nucleus could almost always be seen without destaining, but the vegetative nucleus could not be seen at all unless so treated.

Pollen grains of macadamia were found to germinate satisfactorily in 20 percent sucrose solution. The pollen grains were applied to sucrose-agar media, as described by Maheshwari and Wulff (*18*), or to sucrose solutions covered with water-permeable cellophane as described by La Cour (*14*). In using the first method, the procedure giving best results was: (1) Make a 1.2–2.0 percent solution of agar with sucrose solution, place coverslips into the solution, and drain off the surplus agar solution by applying a blotter to an edge; (2) place the coverslips immediately into a moist chamber made by lining a Petri dish with moist filter paper; (3) after the medium has cooled for several

TABLE 1. PERCENTAGE OF NORMAL POLLEN GRAINS IN SOME VARIETIES OF MACADAMIA.

VARIETY	SOUND GRAINS	UNFILLED GRAINS	FILLED GRAINS
	Number	*Number*	*Percent*
508 (1st sport)	1,018	19	99.17
508 (normal)	975	24	97.60
246 (sport)	688	316	68.52
246 (normal)	968	33	96.70
Y–279 (tetraploid)	979	26	97.41
425	976	26	97.40
336	988	20	98.02
475	979	20	97.99
333	979	21	97.90
37–5	971	29	97.10
404	981	14	98.59
406	980	20	98.00
572	1,082	14	98.72
368	989	9	99.09
Rough-shell (Waipahu)	949	45	95.47
Y–69 (large flowers)	895	105	89.50
Y–69 (normal flowers)	916	85	91.51

minutes, place pollen grains, which have been scraped from a collecting cylinder or obtained directly from unopened buds, on the medium and spread with a camel's hair brush. In the second method, a large drop of sucrose-water solution is placed in a Petri dish and covered with a piece of water-permeable cellophane which has previously been soaked in sucrose solution and partially dried between two pieces of blotting paper. The soaking is necessary to prevent curling of the cellophane.

CALLOSE PLUGS

Callose plugs are always present in the pollen tubes of macadamia (see figure 7). Their apparent function is to enclose the cytoplasm of the pollen tube and so maintain a proper concentration of cytoplasm near the growing tip of the pollen tube. Lacmoid and corallin are both specific stains for callose. The development of the plugs, however, could not be followed with these stains because they are extremely sensitive to callose. Consequently, the internal structure of the pollen tube is not differentiated at the callose plugs. It was found, however, that iron-acetocarmine heavily stains the cytoplasm of the pollen tube but has no affinity for callose. The formation of the plugs can be easily followed with this stain, and the width of the passage left for cytoplasmic flow can be determined.

PROTANDRY

Macadamia, like most other species of the Proteaceae, is protandrous. Tests for germination of pollen grains on styles were carried out in the following manner. First, racemes with buds in which the sepal tips had begun to part were found, and the opened flowers were stripped off. The racemes were tagged, allowed to flower for 2 hours, and stripped of unopened flowers at that time. The flowers were then harvested, at given intervals of time, and allowed to wilt. A stain was prepared by dissolving sodium carbonate and lacmoid dye in water, to saturation, then filtering the solution. The dried style tips were soaked in water for several minutes, crushed, and stained in alkaline lacmoid. These preparations were examined under the microscope for germinated pollen grains.

Lacmoid is a specific stain for callose. According to Stevens (*22*), callose forms a component of the membranes of the pollen grain. After 15 to 30 minutes of staining in lacmoid, pollen grains and tubes became blue. Furthermore, in some cases where the pollen grains had broken off, the dark stained portion of the pollen tube immediately below the pollen grain could be used to determine whether germination had occurred on the flower.

Styles collected within 2 hours after anthesis showed no germinated pollen grains in any variety (table 2). In most varieties tested, germination was first detected at 24 to 26 hours after anthesis. The percentage of flowers with germinated pollen grains increased up to 48 hours after anthesis. Variety 268 had a high percentage with germinated pollen grains at 18 to 20 hours after anthesis.

According to East (*5*), Delpino (*4*) believed that the proteads in general are cross-pollinated because of their protandrous habit. In bagged racemes of *M. ternifolia,* self-pollination occurs in the majority of flowers (see table 4). In bagged racemes, however, there is the objection that the tips of the racemes might have brushed against the bag, which is usually coated with a thin sprinkling of pollen derived from the enclosed raceme.

TABLE 2. NUMBER OF STIGMATA WITH AND WITHOUT GERMINATED POLLEN AT INTERVALS AFTER ANTHESIS.

VARIETY	TIME AFTER ANTHESIS							
	0–2 Hours		18–20 Hours		24–26 Hours		48–50 Hours	
	Germ.	*Ungerm.*	*Germ.*	*Ungerm.*	*Germ.*	*Ungerm.*	*Germ.*	*Ungerm.*
508	0	20	0	25	4	14	28	2
404	0	14	0	20	2	13	18	3
336	0	25	0	18	3	11	14	2
246	0	24	....	....	5	14	22	3
366	0	16	....	....	8	12	32	1
548	0	21	0	24	11	9	18	0
268	0	18	10	19	20	8	30	2

An experiment was therefore carried out on an isolated tree located at Artesian and Young Streets, Honolulu, to determine whether pollen grains deposited immediately after anthesis would adhere to the styles and cause fertilization. Flowers which has just opened, with style still exhibiting the double bend, were marked with India ink and pollinated with pollen from another variety. The racemes were not bagged, in order to allow free play to insects and wind (table 3). It was noted in almost all flowers, except some of those with the double bend, that the terminal pollen clump had disappeared.

TABLE 3. INITIAL SET OF UNTREATED AND CROSS-POLLINATED FLOWERS ON UNBAGGED RACEMES ON AN ISOLATED TREE.

RACEME NUMBER	UNTREATED		CROSS-POLLINATED		
	Number of flowers	Initial set	Pollinating variety	Number of flowers	Initial set
1	216	2	246	12	6
2	213	2	246	10	5
3	173	0	425	10	7
4	219	0	425	7	3
5	143	2	425	7	4
6	169	1	425	8	4

For protandry to cause a high incidence of cross-pollination, either one or another of two conditions must be met. The pollen grains must disperse without adhering to the stigma, or they must lose their viability before the stigma becomes receptive. These conditions are not met in macadamia. Thus, protandry, although it exists in the species, probably does not play the decisive part assigned to it by Delpino (*4*) as a mechanism for increasing cross-fertilization. On the other hand, the delayed germination of the pollen grains may keep the germinating pollen grains of a flower from occupying all the space on a stigmatic surface. This may allow a greater percentage of cross-pollination.

SELF- AND CROSS-POLLINATION

MATERIALS AND METHODS

Racemes were bagged in 8-pound and sometimes in 30-pound paper bags. The bags were fastened to the trees with clothespins. In most cases, a few of the leaves surrounding the raceme had to be trimmed away in order to cover the raceme with the bag. During the 1952 season, pieces of cotton batting were wrapped around the twigs in order to protect them and give a tight seal. During the 1953 season, this practice was discontinued because it was found that cotton batting was not necessary. The bags were marked with the date of bagging and the estimated number of days to anthesis, for example: 3-22 2-3d, meaning bagged on March 22 and expected to open in 2 to 3 days. The date of anthesis was always estimated to be the latest date in designation. Thus, in the example, the estimated date of anthesis is March 25.

Pollen was collected on the inner surface of plastic cylinders, which were made by folding over rectangles of extremely thin and flexible plastic sheets, then gluing the edges together with plastic cement. If a grade of plastic was used which would not melt, these cylinders could be used several times, by killing undesired pollen grains with hot water at 75 to 80 degrees centigrade. Some grades of plastic melted at these temperatures. Later, these sheets of plastic were no longer available on the market, and florists' waxed tissue paper was used as a substitute. It was superior in most respects to plastic. The material was cheaper, folded easily, and could be glued together with rubber cement. The only difficulty with this material was that the wax tended to melt on extremely hot days and would glue the sides of the cylinder together. These cylinders, of course, could be used only once.

In collecting pollen, racemes which had been bagged before anthesis were guided into the cylinder, and the cylinder was gently rubbed against the flowers, causing the pollen masses to cling to the slightly sticky material. To pollinate, the cylinder, with adhering pollen, was rubbed on a raceme which had been allowed to flower in a paper bag. The raceme was then rebagged. Pollinated cylinders were kept separate, according to pollen variety, in plastic sandwich boxes which were 4½ inches by 4 inches in size. The pollen cylinders were made to fit in this space without folding. Pollen stored in this way showed no apparent loss in viability up to 3 days after collection. No attempt was made to determine the maximum length of time that the pollen remained viable.

Emasculation of the flowers was not practiced extensively because of the slowness of the technique required and because of the normally low percentage set which occurs in macadamia. However, a satisfactory, although rather tedious, method of emasculation was developed. Buds at 7 to 8 days before anthesis were selected. One side was carefully slit with a needle, care being taken not to injure the style. The resulting flap was cut and removed with a pair of sharp-pointed forceps; then the rest of the perianth was removed in several pieces. A necessary step in this procedure is that the initial slit with the needle must pass through the bud cap; otherwise, the style tip will break off with the attached anthers.

As mentioned previously, a normally developed macadamia raceme may bear from 100 to 300 flowers. Considering the low percentage set which characterizes the species, it was thought impractical to count the number of flowers on each raceme. A count was taken of flowers of a few varieties to see if any

correlation existed between flower number and length of raceme, but it was soon obvious that such a correlation, if present, would be of such low value that it would be useless for giving a rough estimate of the flower number on any given raceme. Fruit set was accordingly counted as set per raceme instead of percentage of flowers set.

Although, if unfertilized, many flowers undergo abscission 6 to 8 days after the sepals fall, it was found that the fall of the flowers is not correlated with lack of pollination, since most of the fallen flowers collected from the bag had germinated pollen grains in the stigmatic surface. It was also observed that after this initial drop of the presumably unfertilized flowers, the ovaries of the remaining young fruits enlarge. When sections were made, most were found to be fertilized and producing endosperm tissue, although some were abortive. The initial set is, therefore, a reliable measure of fertilization.

In cross racemes, initial set was recorded at 15 to 20 days after cross-pollination, while in self-pollinated racemes, initial set was recorded at 15 to 20 days after anthesis. In a few cases, counts were taken as early as 12 days after anthesis, but this was done only when the young fruits were found to be definitely enlarged at the ovaries. For any given flower, initial set may safely be recorded at 12 days after anthesis, but the presence of varieties with a pronounced tapering habit of blooming makes 15 to 20 days after anthesis the better period for recording these data.

POLLEN GERMINATION ON THE STYLE

All racemes of macadamia showed a high percentage of flowers with germinated pollen grains when they were examined about 48 hours after anthesis (see table 4). It was therefore considered that self-pollination need not be induced by manipulation but that merely bagging the racemes was sufficient. It will later herein be shown that manipulation of bagged flowers with pollinating cylinders does not markedly change the initial set.

TABLE 4. FLOWERS WITH GERMINATED POLLEN GRAINS AND NON-GERMINATED POLLEN GRAINS IN BAGGED RACEMES OF MACADAMIA.

VARIETY	NUMBER OF FLOWERS		PERCENT OF FLOWERS WITH GERMINATED POLLEN
	Germinated	Ungerminated	
C-130	62	1	98.41
37-15	20	5	80.00
508	22	3	88.00
404	20	3	86.95
246	31	6	83.78
37-6	30	2	93.75
406	34	4	89.47
538	42	5	89.36
37-4	22	2	91.66
37-14	38	4	90.48
268	49	4	92.45

EFFECT OF SELF-POLLINATION

Since macadamia is apparently self-pollinating, some racemes were bagged, as described earlier, and the initial set was recorded. The results are presented in tables 5 and 6.

TABLE 5. FREQUENCY DISTRIBUTION OF INITIAL SETS OF SELF-POLLINATED RACEMES. NUTRIDGE, 1953.

VARIETY	NUMBER OF FRUITS PER RACEME											
	0	1	2	3	4	5	6	7	8	9	10	More than 10
A-98	54	5	1									
Y-17	48	3		1								
C-18	32	3										
B-1	36	4	2									
A-95	24	2	1	2								
Y-14	18	4	2	2	1							
A-100	14											
Y-35	18	1	1									
C-695	16	5	3	3	1							
Y-282	13	5										
Y-7	36											
475	18	9	4	1								
Y-15	13											1
Y-16	12	6	6	2	1							
Y-69	17	3										
Y-51	15		1									
C-652	9		1		1							
C-679	8	4	2					1				
Y-24	13	4	3	1								
B-6	10											
841-A	8	2	4		1		1	1				
Y-275	8	1										
A-92	11	8	1	1		1	1		1	2		1
A-104	8	3	1	1				2	1	1		1
Y-279	6	8	3	1		1						
X-103	7	1	3	1	1	1						
B-11	7		1	1								
B-5	6	4										
C-248	2	3	3	1	2	1	1					
C-25	6	1	1									
C-785	9									1		
Y-253	5	2	2		1							
C-650	1		1						2	1	1	4
X-123				1							1	11

TABLE 6. FREQUENCY DISTRIBUTION OF INITIAL SETS OF SELF-POLLINATED RACEMES. WAIPAHU, 1953.

VARIETY	NUMBER OF FRUITS PER RACEME											
	0	1	2	3	4	5	6	7	8	9	10	More than 10
246	101	45	19	12	8	13	11	4	1	3	1	4
508	79	41	26	13	10	8	7	5	2	2	2	5
425	103	8	4	1	1							
336	70	15	2	6	2	1	1					
37-4	58	15	6	6	5	2	1					
37-53	27	14	6	5	4	1	2	1	1		2	1
404	90	16	5	1	1							
274	29	6	1	5	3	2						
538	47	8	1	1			1					
368	9	6	4	7	2	7		1	1		2	2
572	62	19	7	3	1							
406	40	9			1	1						
37-6	72	9	2	1								
37-15	89	27	8	3	1	1						2
548	20	11	6	6	2	7	6		1		2	9
268	1				1	1	1	3	2	4		41
37-14	2		1	1	1	1	4	2	2		4	31
366	3	1	3	2	2	4	1	1	2	1	3	23

It is clear, from the data, that the majority of varieties tested were partially self-sterile,[1] since the modal initial set of the racemes was zero in most cases. In a few varieties, however, the modal initial set is much higher, and these varieties may be classified as self-fertile.

EFFECT OF CROSS-POLLINATION

Since cross-pollination was carried out without emasculation, no attempt was made to demonstrate cross-fertility in the varieties known to be self-fertile. However, in other varieties many crosses were made, using the pollinating cylinders. The results are shown in tables 7, 8, and 9.

It is clear, from the data, that most crossed racemes show a large increase in initial set over selfed racemes of the partially self-incompatible varieties. In most cases, they exceed the highest initial set obtained in the bagged racemes. In several crosses, no initial set was obtained, but these were all single-raceme crosses which were made relatively late in the season when many varieties with a normally high initial set began to show decreased initial set. These crosses could not be repeated. None of the reciprocal crosses of the nonsetting crosses were incompatible. In every variety tested, the initial set of the partially self-in-

[1]The term self-sterility is here used interchangeably with the term self-incompatibility. Incompatibility denotes interference with pollen-tube growth in the style and a consequent failure of fertilization; whereas, sterility denotes failure of the embryo after fertilization. Since both conditions may occur simultaneously, according to Brink and Cooper (*2*), or separately, and since it was not proved which condition occurred in macadamia, both terms are used.

TABLE 7. INITIAL SET AND LATE SET* ON CROSS-POLLINATED RACEMES.† WAIPAHU, 1953.

FEMALE X		INITIAL SET	LATE SET
246			
x	508	78	1
		42	
		72	2
		52	0
		45	4
		64	6
		29	2
		33	
		21	
		10	
		15	
x	425	57	3
		24	2
		62	1
		5	
x	336	31	2
		45	0
		25	1
		19	0
		8	
		10	
x	37-15	29	1
		16	
		12	
x	404	12	0
		10	0
x	475	19	1
x	37-14	20	
		24	
x	268	30	
x	572	19	
x	37-4	22	1
x	368	11	
x	37-6	19	1
x	274	20	1
x	548	17	1
x	366	5	
x	37-53	7	
508			
x	246	44	0
		56	1

FEMALE X		INITIAL SET	LATE SET
508			
		35	1
		49	0
		37	1
		65	1
		19	3
		22	2
		51	0
		34	0
		46	0
		45	1
		21	2
		23	2
		16	
		6	
x	425	35	0
		22	
		19	
		0	
		36	0
		57	0
		24	0
		33	0
		45	1
		43	2
		31	0
x	336	40	0
		10	
		50	2
		41	4
		33	0
		50	1
x	475	48	2
		57	
x	37-15	28	1
x	368	15	
x	548	29	
x	268	21	
x	572	24	1
x	37-14	21	
x	37-6	36	
x	538	1	

FEMALE X		INITIAL SET	LATE SET
508			
		6	
		8	
x	37-53	25	2
x	406	25	2
		12	
x	274	17	
		12	
x	425	28	3
425			
x	246	21	0
		23	0
		18	1
		13	2
x	508	29	
		14	0
		43	1
		26	0
		36	0
		43	0
		11	0
		35	0
x	A-98	10	0
x	404	17	
x	336	4	
		21	0
		20	8
		28	2
		18	1
x	37-15	16	0
x	274	24	
x	37-4	3	
x	406		
x	548	10	
368			
x	274	11	
x	37-15	16	
x	37-4	17	
		15	
x	404	14	
		10	

* Forty-five to 70 days after anthesis.
† Where no numbers appear, no counts were made.

TABLE 7. (Cont'd.)

FEMALE	x	INITIAL SET	LATE SET
368			
		11	
x	A-95	24	
x	268	13	
x	37-6	21	
x	406	11	
x	246	12	
x	366	19	
x	37-53	19	
x	37-14	12	
x	548	13	
x	425	10	
x	37-14	11	
274			
x	37-4	18	0
x	425	60	
x	404	35	0
x	406	23	
x	37-14	21	3
x	548	39	
x	368	63	
x	37-6	24	2
x	246	49	
		33	
x	336	17	
x	37-53	59	
x	336	12	
x	572	50	
x	Y-279	20	
572			
x	548	12	
x	37-15	20	
x	336	12	
x	246	10	
x	37-6	27	
x	508	16	
x	425	5	
		16	
x	37-14	15	
x	368	19	
x	404	18	
x	37-53	23	
x	274	4	

FEMALE	x	INITIAL SET	LATE SET
572			
x	538	14	
x	268	15	
x	368	19	
548			
x	404	29	
x	538	19	
x	406	25	
x	37-6	38	
		29	
x	37-53	11	
x		37	
x	368	27	
x	37-4	42	
x	268	27	
x	274	34	
x	37-15	20	
x	37-14	5	
x	508	28	
x	572	18	
x	366	27	
x	538	14	
x	246	23	
x	366	10	
37-6			
x	538	26	4
		17	
x	406	26	5
		25	2
x	548	25	2
x	37-4	40	3
x	368	13	0
x	37-15	30	2
x	37-14	24	2
x	37-53	31	0
x	572	15	
		28	
x	274	19	
x	366	62	
x	336	23	
x	404	13	
		16	
x	268	15	

FEMALE	x	INITIAL SET	LATE SET
37-6			
x	425	10	
		4	
x	508	31	
x	246	11	
		0	
x	548	19	
406			
x	37-6	31	6
x	548	24	6
x	538	13	0
x	336	58	1
x	37-53	30	0
x	841-A	37	2
x	404	7	
		30	
x	37-15	27	
x	336	23	
x	37-4	25	
x	368	12	
x	274	14	
x	366	14	
x	37-14	19	
x	572	24	
x	246	18	
x	425	27	
x	268	21	
x	37-6	14	
x	508	7	
		14	
		21	
425			
x	572	11	
x	268	4	
x	37-6	9	
x	368	5	
336			
x	246	26	1
		24	1
x	508	12	2
		15	0
		16	0
x	425	39	2

TABLE 7. (Cont'd.)

FEMALE X	INITIAL SET	LATE SET
336		
	14	
	8	0
x 37-53	41	4
	32	
x 406	31	1
x 548	17	
x 274	31	
x 366	19	0
x 37-14	10	
	5	
x 404	15	
x 368	28	
x 37-15	55	
x 572	0	
x 538	2	
x 37-6	10	
x 37-4	7	
37-15		
x 37-14	31	2
x 274	22	1
x 268	36	0
x 274	39	1
x 538	10	0
	5	1
x 368	16	
x A-104	0	
	12	
	15	
	12	
x 37-53	15	
x 336	14	
x	12	
x 508	9	
x A-98	14	
x 406	11	
x 404	17	
x 425	15	
x 572	13	
x 336	12	
x 37-6	14	

FEMALE X	INITIAL SET	LATE SET
37-4	15	
x 37-15	21	1
	14	2
x 274	16	
x A-104	17	1
x A-95	22	
x 548	16	
x 274	22	
x A-98	34	
x 268	38	
x 246	36	
x 406	10	
x 538	11	
x 366	24	
x 37-53	9	
x 336	7	
x 425	12	
x 368	16	
x 37-14	18	
x 368	14	
x 572	12	
538		
x 406	73	
	26	1
x 404	39	0
x 274	58	0
	65	0
x 548	70	1
x 37-6	36	
x 37-15	35	
x 336	53	
x 37-53	44	
x 366	22	
x 268	26	
x 572	29	
x 37-4	47	
x 425	52	
	34	
	14	
x 368	63	
x 508	10	
x 37-14	12	

FEMALE X	INITIAL SET	LATE SET
37-53		
x 37-15	28	
x 37-6	17	
x 406	11	
x 37-4	12	
x 268	17	
x A-95	19	
x 368	13	
x 538	10	
x 404	20	
x 37-14	33	
x 274	14	
x 425	21	
	19	
x 246	23	
x 336	14	
x 366	32	
x 508	36	
	18	
x 548	29	
	20	
x 572	21	
404		
x 37-15	1	
x 37-4	23	0
x A-104	23	0
x 538	41	
x 548	52	0
x A-98	39	
x 268	50	
x 37-14	34	
x A-95	31	
x 366	14	
x 425	42	
x 246	4	
	7	
x 37-53	23	
x 366	27	
x 406	14	
x 572	15	
x 368	9	

TABLE 8. INITIAL SET AND LATE SET* AFTER SELF-POLLINATION. WAIPAHU, 1953.

VARIETY	INITIAL SET	LATE SET †
246	1	0(23)
	1	1(3)
	2	0(14)
	2	1(3)
	3	0(6)
	4	0(5)
	4	1(1)
	5	0(6)
	5	1(2)
	5	2(1)
	6	0(4)
	6	1(4)
	6	2(1)
	7	0(2)
	8	1(1)
	9	0(1)
	10	1(1)
	11	0(1)
	12	0(1)
	14	0(1)
	14	1(1)
	14	2(1)
508	1	0(17)
	1	1(9)
	2	0(8)
	2	1(2)
	3	0(9)
	3	1(1)
	3	2(2)
	4	0(4)
	4	1(2)
	4	2(2)
	5	0(2)
	5	1(1)
	5	2(1)
	6	0(3)
	6	1(1)
	6	2(1)
	7	0(2)
	7	1(2)
	8	2(1)
	9	0(1)
	9	1(1)
508	10	0(1)
	10	2(1)
	12	0(1)
	12	2(1)
425	1	0(2)
	2	0(1)
274	3	1(1)
	4	2(1)
37-6	1	0(2)
37-4	2	0(1)
404	1	0(5)
	2	0(3)
	4	0(1)
406	1	0(4)
	6	0(1)
37-15	1	0(8)
	1	1(3)
	2	0(3)
	2	2(1)
	3	2(1)
	4	0(1)
	5	2(1)
	7	0(1)
	14	0(1)
268	4	0
	27	0
	13	0
	12	0
	22	0
	28	0
	9	0
	15	0
	18	0
	14	0
	18	0
	18	0
268	12	0
	23	1
	12	1
	13	1
	17	1
	20	1
	18	1
	22	1
	16	1
	28	1
	33	1
	9	1
	10	1
	15	1
	17	1
	13	2
	29	2
	20	2
	35	2
	20	2
	19	2
	24	2
	25	2
	18	2
	25	2
	25	3
	36	6
37-14	7	0
	40	0
	21	0
	18	0
	36	0
	15	0
	14	0
	15	0
	19	0
	13	0
	10	0
	2	0
	11	0
	8	0
	13	1
	16	1
	29	1

* Forty-five to 70 days.

† In parentheses: number of racemes.

TABLE 8. (Cont'd.)

VARIETY	INITIAL SET	LATE SET †	VARIETY	INITIAL SET	LATE SET †	VARIETY	INITIAL SET	LATE SET †
37-14	10	1	366	23	0	366	17	1
	8	1	(Cont'd.)	21	0	(Cont'd.)	21	1
	16	2		19	0		17	1
	39	2		23	0		16	1
	4	2		11	0		16	1
	12	2		13	0		10	1
	19	2		19	0		16	1
	36	2		13	0		8	1
	23	3		10	0		6	1
				8	0		26	2
366	15	0		11	0		10	2
	5	0		17	0		29	2

compatible varieties could be raised to levels near or above those of the self-fertile varieties, by cross-pollinating with the pollinating cylinders. In these cross-pollinated racemes, as in the self-pollinated racemes, the initial set varied tremendously. This variation was far greater than that expected by considering solely the variation in the number of flowers in the racemes, since at least 90 percent of these could be placed in the range of from 100 to 275 flowers per raceme. The cause of this fluctuation in the initial set is unknown, although there are suggestions that it may be related to plant vigor and nutrition.

Although it was not possible to record harvest sets, some data on set per raceme were recorded at 45 to 70 days after anthesis. At 60 days, in all varieties tested, the cotyledons occupy the major portion of the interior of the testa. The growth of the cotyledons seems to occur quite rapidly and apparently is initiated between 45 and 60 days after anthesis. Tables 7 and 8 show this later set, as well as initial set in several combinations of cross- and self-pollinations.

There is no evidence to show, once initial set has occurred, that the variety of the pollinating parent has any influence on the harvest set. Fruits from self-pollinated, partially self-sterile varieties, and self-fertile varieties may reach maturity, and so may fruits from cross-pollinated racemes. At any rate, from the data available, the four commercial varieties at Waipahu are mutually cross-compatible when initial set is considered. The variety 475 at Nutridge is cross-compatible with 246 and 508, but crosses were not attempted with 425 or 336. However, it is cross-compatible, as a female, to all four of the named varieties at Waipahu.

COMPARISON OF SELF- AND CROSS-POLLINATION

In table 10, the effects of self- and cross-pollination on 18 varieties at Waipahu are summarized. In the column entitled Treatment, three classifications are listed to cover most of the varieties: Selfed, Manipulated, and Crossed.

"Selfed" refers to racemes which had been merely bagged before anthesis, with no subsequent treatment. "Manipulated" refers to racemes from which pollen had been collected with pollinating cylinders or to those which had been self-pollinated with pollen collected from another raceme of the same variety. "Crossed" refers to racemes which had been pollinated with pollen gathered

TABLE 9. INITIAL SETS RESULTING FROM CROSS-POLLINATION. NUTRIDGE, 1953.

CROSS	SET
A-98	
x B-1	10
x A-95	10
x A-92	9
	10
x B-22	1
x 475	18
x A-100	2
Y-17	
x Y-14	15
x C-18	20
x Y-16	17
x Y-69	9
x C-32	12
x Y-24	4
C-18	
x 425	68
x C-785	4
x C-180	15
x Y-17	22
B-1	
x B-30	75
	36
x Y-279	17
x 508	19
x 37-15	32
A-95	
x A-99	14
x A-92	18
	14
x A-100	24
x Y-16	9
	7
Y-14	
x Y-13	11
x C-695	4
x C-18	37
	11
	10
x Y-69	7
	0
x Y-51	8
Y-35	
x C-18	9
A-100	
x A-98	25
	10
x A-95	10
C-695	
x C-679	31
x A-95	35
x A-92	18
x A-74	4
x Y-14	6
x C-18	12
x A-98	11
x Y-16	33
Y-282	
x C-650	27
x C-434	49
Y-7	
x Y-69	35
x Y-24	32
475	
x 246	44
	31
	46
	61
	123
x 425	79
x 508	73
	47
	119
x 336	62
Y-69	
x Y-14	26
	27
x Y-24	0
	8
x Y-51	20
	20
Y-16	
x A-74	10
x C-18	14
Y-652	
x C-679	39
x C-650	45
x C-650	36
x B-30	18
x C-14	23
x C-841	14
C-679	
x C-14	44
x C-841	30
Y-24	
x Y-51	16
	26
	21
x C-32	19
x Y-14	27
x C-33	21
x Y-69	48
	59
x Y-282	24
x C-248	14
x C-18	27
C-841-A	
x C-434	35
x C-18	6
Y-275	
x 425	25
x C-841	21
A-92	
x B-22	32
x A-98	44
x A-95	32
x A-100	14
x A-99	25
A-104	
x A-98	49
	39
x A-99	71
x B-22	52
x A-102	74
x Y-7	25
B-11	
x 246	60
x B-5	52
	7
	16
C-785	
x 425	15
x C-18	30
x Y-14	6
C-14	
x C-841	7
x C-652	34
x C-679	27
Y-272	
x Y-282	15
Y-273	
x Y-272	32
Y-80	
x C-10	
Y-13	
x Y-14	
X-128	
x Y-278	35
x C-650	50
x C-652	30
C-434	
x 425	18
x C-18	21
x Y-17	5
x C-683	6
x Y-14	3
B-5	
x B-22	5
x 37-15	2
x 246	5
x 508	1
x B-1	8

from another variety. Initial set, as indicated previously, refers to young fruit at 15 to 20 days after anthesis. In each case, bagging preceded and followed treatment.

In 15 of the 18 varieties, the initial set produced on selfed and manipulated racemes was low. In these varieties, the crossed racemes show a striking increase in initial set when compared to both the selfed and manipulated racemes. In the other three varieties, the initial set resulting from all three treatments was relatively high.

EFFECT OF SELF- AND CROSS-POLLINATION ON THE COMMERCIAL VARIETIES

Of the seven commercial varieties, only five were available for crossing. These were varieties 246, 425, 508, 336, and 475. The original trees of two other clones, 333 and 389, were located at Nutridge, but in both cases the flowering

TABLE 10. INITIAL SET IN SELFED, MANIPULATED, AND CROSS-POLLINATED VARIETIES OF MACADAMIA. WAIPAHU, 1953.

VARIETY	TREATMENT	TOTAL INITIAL SET	NUMBER OF RACEMES	MEAN INITIAL SET	PERCENTAGE OF RACEMES WITH NO SET
246	Selfed	408	222	1.83	45.49
	Manipulated	14	15	0.95	60.00
	Crossed	1,042	39	26.72	0.00
508	Selfed	412	200	2.06	39.50
	Manipulated	29	12	2.41	16.66
	Crossed	1,651	51	32.37	2.00
425	Selfed	23	117	0.19	88.03
	Manipulated	4	6	0.66	66.66
	Crossed	494	28	17.64	3.57
336	Selfed	56	97	0.57	72.16
	Manipulated	11	6	1.50	33.33
	Crossed	395	21	18.08	4.16
37-4	Selfed	81	93	0.29	71.60
	Manipulated	3	2	0.71	50.00
	Crossed	395	21	27.05	0.00
37-53	Selfed	121	64	1.89	42.18
	Manipulated	11	18	3.66	33.33
	Crossed	410	3	22.77	0.00
404	Selfed	33	113	0.29	79.64
	Manipulated	5	7	0.71	42.86
	Crossed	487	18	27.05	0.00
274	Selfed	53	47	1.13	61.70
	Manipulated	7	3	2.33	33.33
	Crossed	503	14	35.93	0.00

TABLE 10. (Cont'd.)

VARIETY	TREATMENT	TOTAL INITIAL SET	NUMBER OF RACEMES	MEAN INITIAL SET	PERCENTAGE OF RACEMES WITH NO SET
538	Selfed	13	57	0.23	82.45
	Manipulated	0	4	0.00	100.00
	Crossed	807	20	40.35	0.00
368	Selfed	116	50	2.32	18.00
	Crossed	257	18	14.28	0.00
572	Selfed	46	92	0.50	67.39
	Manipulated	1	3	0.33	66.66
	Crossed	271	19	14.26	5.26
406	Selfed	28	52	0.54	76.92
	Manipulated	0	2	0.00	100.00
	Crossed	230	13	17.69	0.00
37-6	Selfed	5	84	0.06	85.71
	Manipulated	0	5	0.00	100.00
	Crossed	552	22	25.09	4.54
37-15	Selfed	75	130	0.58	68.46
	Manipulated	17	11	1.54	36.35
	Crossed	367	22	16.68	0.00
548	Selfed	286	70	4.08	28.57
	Crossed	520	19	27.37	0.00
268	Selfed	877	54	16.24	1.85
	Manipulated	150	6	25.00	0.00
	Crossed	54	4	13.50	0.00
37-14	Selfed	760	49	15.51	4.08
	Manipulated	216	14	15.43	7.14
	Crossed	12	1	12.00	0.00
366	Selfed	503	46	10.93	6.52
	Manipulated	154	5	10.26	0.00
	Crossed	9	1	9.00	0.00

branches were too high to be worked. Brief descriptions of the condition of the trees, their response to self– and cross-pollination, are hereafter given.

VARIETY 246

Variety 246 was represented by seven trees at Waipahu. All of the trees were located in poor soil. They were in poor condition, with chlorotic leaves and many dead branches. The flowers in this variety are characterized by having green bud caps almost until anthesis. The variety is partially self-incompatible. Of 222 racemes bagged without subsequent treatment, 45.49 percent had no initial set. The mean set per raceme was 1.83. Of 39 racemes which were bagged and subsequently cross-pollinated, all had some initial set, and the mean initial set was 26.72 per raceme.

VARIETY 508

Variety 508 was represented by a block of four trees at Waipahu, near an irrigation ditch, in a very windy location. The trees were short and ranged from 12 to 15 feet at 15 years after planting. The soil depth at the location of the trees was 3 feet, where the irrigation ditch runs over a bed of solid rock. The variety is partially self-incompatible, and of 200 bagged racemes, 39.50 percent had no initial set. The mean set per raceme was 2.06. Of 51 racemes that were bagged and subsequently cross-pollinated, 2.0 percent had no set, and the mean initial set was 32.37 fruits per raceme.

VARIETY 425

Variety 425 was represented at Waipahu by three trees in very poor condition. The estimated heights of the three trees were 8, 6, and 12 feet. One of the trees was partially recumbent, and all three showed signs of chlorosis, drought, and severe wind damage. Nevertheless, some of the racemes had the grape-cluster harvest characteristic set of the variety. The variety is partially self-incompatible, and of 117 bagged racemes, 88.03 percent had no initial set. The mean set per raceme was 0.19. Of 28 racemes that were bagged and subsequently cross-pollinated, 3.57 percent had no initial set, and the mean initial set was 17.64.

VARIETY 336

Variety 336 was represented by nine relatively thrifty trees at Waipahu. The variety is susceptible to anthracnose to some extent, and many mumified fruits were observed on the trees. The unfertilized flowers on bagged racemes tended to adhere to the rachis instead of falling, even until the time when initial set was recorded. The variety is partially self-incompatible. Of 97 bagged racemes, 72.16 percent had no initial set, and the mean set per raceme was 0.57. Of 21 racemes that were bagged and subsequently cross-pollinated, 4.16 percent had no initial set, and the mean initial set was 18.08.

VARIETY 475

Variety 475 was represented by one tree at Nutridge. It was about 30 feet high. The tree was located near a windbreak and overhanging fruit trees, so that it probably received less than optimum sunlight. The variety is partially self-incompatible. Of 33 bagged racemes, 54.54 percent had no initial set, and the mean set per raceme was 0.94. Of 10 racemes that were bagged and subsequently cross-pollinated, none failed to show an initial set, and the mean initial set per raceme was 68.5.

Thus, all of the five commercial varieties tested may be considered to be partially self-fertile. Additionally, since their initial set is low in contrast to the set resulting from cross-pollination, it may also be concluded that they show a marked response to cross-pollination.

RATE OF FALL OF THE INITIAL SET

The high initial sets of cross-pollinated macadamia underwent a rapid drop during the first month after anthesis. A few of the fruits which fell during this early drop were sectioned. Although some of these were aborted, others were apparently normal.

As mentioned previously, the rachis of the macadamia raceme first shows conspicuous enlargement sometime between 30 and 45 days after anthesis, and it does not form mature bark until 45 to 69 days after anthesis. Furthermore,

TABLE 11. NUMBER OF FRUITS PER RACEME REMAINING AT VARIOUS TIMES AFTER ANTHESIS.

PART A

VARIETY AND POLLINATION CROSS	NUMBER OF DAYS AFTER POLLINATION				
	16 *f/r**	22 *f/r**	33 *f/r**	42 *f/r**	51 *f/r**
508 x					
336	50	31	9	3	2
	41	24	5	4	4
	33	17	6	1	0
	50	20	3	1	1
	68	23	2	2	1
425	36	27	6	2	0
	57	32	3	0	0
	24	17	3	0	
	33	13	3	0	
	45	15	4	3	1
	43	22	2	2	2
	31	18	0		
	28	11	4	3	3
246	21	15	3	2	2
	23	10	2	2	2
508	1	1	0		
	3	2	1	1	0
	5			3	1
	2			0	
	3			0	
	1	1	1	0	
	1	1	1	1	1
	1	0			
	1	1	1	0	
	2	0			
	3	3	2	0	
	2	2	0		
	6	5	1	1	1
	10	1	1	0	
	2	2	2	0	
	4	4	1	0	
	12	11	0		
	3	1	1	0	

* Fruits per raceme.

TABLE 11. PART A. (Cont'd.)

VARIETY AND POLLINATION CROSS	NUMBER OF DAYS AFTER POLLINATION				
	16 *f/r**	22 *f/r**	33 *f/r**	42 *f/r**	51 *f/r**
508 x					
508	1	1	1	0	
	3	3	1	0	
	1	1	0		
	1	0			
	1	1	0		

* Fruits per raceme.

PART B

VARIETY AND POLLINATION CROSS	NUMBER OF DAYS AFTER POLLINATION				
	17 *f/r**	26 *f/r**	32 *f/r**	45 *f/r**	57 *f/r**
406 x					
37-6	31	14	14	12	6
548	24	14	9	9	6
538	13	4	1	0	
336	58	4	2	2	1
37-53	30	6	3	1	0
841-A	37	9	4	4	2
406 (bagged)	1			0	
	6				0

* Fruits per raceme.

PART C

VARIETY AND POLLINATION CROSS	NUMBER OF DAYS AFTER POLLINATION						
	17 *f/r**	31 *f/r**	36 *f/r**	44 *f/r**	49 *f/r**	51 *f/r**	56 *f/r**
37-6 x							
538	26		6		4		4
406	26		7		5		5
548	25		5		3		3
0	1		1		1		0
37-4	40	10		5		3	
368	45	13		4		0†	
37-15	30	9		2		2	
37-14	24	8		2		2	
406	28	8		3		3	
37-53	31	12		3		0	
37-6 (bagged)	2			0			
	1			0			

* Fruits per raceme.

† Broken off.

PART D

VARIETY AND POLLINATION CROSS	NUMBER OF DAYS AFTER POLLINATION			
	16 *f/r**	21 *f/r**	28 *f/r**	45 *f/r**
475 x				
246	44	37	11	0
	31	27	13	3
	46	31	11	2
	61	47	7	0
425	123	77	7	2
	79	24	6	0
508	73	37	10	2
	119	27	3	1
336	62	42	15	7
475 (bagged)	1	1	0	
	15	9	2	0
	1	1	1	1
	1	0		
	2	1	1	0
	1	1	1	0
	1	0	1	0
	2	2		

* Fruits per raceme.

fruits on racemes with low initial sets tend to adhere to the style, without the rapid drop characteristic of racemes with high initial set. The data in table 11 illustrate this fact. In the light of these observations, it seems likely that the cause of this early drop is nutritional.

EFFECT OF THE TIME OF BAGGING ON INITIAL SET

Although variety 508 was highly self-compatible in the year 1952, it was noted in the first racemes bagged in 1953 that they had a considerably larger initial set than in the previous year. As the season progressed, the initial sets gradually lessened. This difference is seen in table 12, where intial sets of racemes bagged in bud, but otherwise untreated, are shown in a frequency distribution.

The mean initial set per raceme shows considerable difference between the two periods of bagging. The difference is much more striking in variety 508 than in variety 246. The cause of this difference in set in different months is not known.

POLLEN DISTRIBUTION

INSECTS

The occurrence of self-incompatibility in many varieties of macadamia and the high initial set which occurs both in open-pollinated racemes and in bagged and cross-pollinated racemes indicate that some highly efficient pollen vector is present. Several writers believed that cross-pollination in the Proteaceae was effected mainly by birds, but others, such as Engler and Prantl (*7*) in 1894, believed the pollinators to be insects. During the field work on this entire problem, no bird was ever observed working the flowers of macadamia.

TABLE 12. EFFECT OF TIME OF BAGGING ON FREQUENCY DISTRIBUTION IN INITIAL SET OF UNTREATED, POLLINATED RACEMES. WAIPAHU, 1953.

VARIETY	MONTH BAGGED	INITIAL SET PER RACEME															TOTAL SET	TOTAL RACEMES	MEAN INITIAL SET	RACEMES WITH NO SET
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14				
																				Per-cent
508	March	19	22	15	12	7	6	6	3	2	2	1		4	1		308	100	3.08	19.0
	April and May	45	12	5	1		1		1								32	65	0.49	69.23
246	March	35	22	5	5	5	10	9	3	1	2		1			3	271	98	2.76	35.71
	April	42	15	3	6	2	2	2	1		1						85	74	1.15	56.75

INSECTS WORKING MACADAMIA FLOWERS

A great number of insect species sporadically visit the flowers of macadamia. However, the most frequent insect visitors, found on practically every trip to the orchard, were the honeybee (*Apis mellifera*) and the syrphid fly (*Volucella obesa*). Other syrphids (*Lathryopthalmus arvorum* and *L. aemea*) were found almost as frequently as *V. obesa*. A species of thrips also was almost always found on the flowers.

It was evident that the syrphids are slower workers than the honeybees, and the syrphids vary enormously in population during the year. Some degree of cross-pollination might be caused by the syrphids, especially by *V. obesa,* which is abundant, a strong flier, and large enough that it comes into occasional contact with the terminal pollen clumps of macadamia flowers. All of the syrphids mentioned were at times found covered with pollen grains, and so were the honeybees.

HONEYBEES

The honeybees are the most abundant and industrious of all of the insects that work the flowers of macadamia. These may be divided into two types, the nectar collectors and the pollen collectors.

The nectar-collecting bees are usually more numerous but are relatively slower working. They also come relatively infrequently into contact with the stigmatic portion of the style. However, in racemes in which pollen clumps are abundant, such as those that had been bagged and allowed to flower in the bag, the nectar-collecting honeybees may become liberally covered with pollen grains. This may occur from contacts with the terminal clumps by landing on the racemes, by brushing wings on the style tips, or by crawling over and forcing down a flower. It is possible that foreign pollen adhering to the bee may be dislodged in these activities and find its way to a stigma through the air, without direct contact of the bee with the stigmatic surface.

The pollen-collecting honeybees, on the other hand, work extremely rapidly and appear at times to be in a state of frenzy. Some individuals frequently make short flights away from the raceme and return within a few seconds. The pollen collectors invariably work the nectaries of the flowers. In racemes with relatively short styles, these bees appear merely to walk over the flowers, at a higher level than the nectar collectors and the syrphids, and they collect pollen on their body parts in this manner. Where racemes occur with relatively long styles, the bees clasp the styles with their legs and work the terminal pollen clumps with their mouth parts.

Frequently, the pollen collectors make short hovering flights up and down the raceme, work their legs and mouth parts together, and apparently transfer their pollen grains to the pollen baskets on their hind tibiae. During these hovering flights, it appears that the bees are searching for unworked pollen clumps, because their head parts are usually within an inch of the style tips. Upon landing, after these short flights, the bees frequently grasp a style with their leg parts and bring their mouth parts into contact with or in close proximity to the style tips. However, more often than not, they select styles which have been stripped of their pollen clumps, after passing several with intact pollen clumps.

POLLEN PELLETS COLLECTED AT THE HIVE

Five hives are located at the Nutridge orchard. According to the manager of the company which operates the orchard, the hives were originally put in to increase cross-pollination but had not been maintained recently because there was no proof that pollination by bees was necessary. At the Honokaa orchard, according to its manager, a large number of beehives were formerly scattered throughout the orchard, but in recent years the practice has not been continued because it has interfered with harvesting operations. At both the Waipahu orchard and the Honokaa orchard, where no beehives are maintained, there is an abundant bee population. It is probable that in the small or scattered seedling orchards, which make up most of the plantings in the Territory, wild honeybees take care of most of the pollination requirements. In extensive plantings with no uncleared land for cover, some provision for beekeeping may be necessary.

From observations made at the trees, it seemed evident that pollen-collecting bees are the most efficient dispersers of pollen clumps and are, therefore, presumably the most efficient pollen vectors. To test this, a count was taken of the percentage of macadamia pollen in pollen pellets trapped at the hive. In order to trap pollen pellets, a trap devised by Kremer (*13*) was used for this purpose. The pollen trap was left in front of the hive for at least 8 hours. The collected pollen pellets were then screened with a 16-mesh screen, and a sample was taken of the pellets which were too large to pass through the screen. The pellets were arranged on a glass slide, pressed down with another slide, and examined under a microscope at 100 diameters magnification.

Macadamia pollen grains were easily distinguished from the pollen grains of other species. The macadamia pollen grains are triangular in outline and have definite, though rather small, germ lobes. The pollen grains of the only other species of Proteaceae which is present in the neighborhood are much larger than those of macadamia. There also was an unidentified species with triangular and slightly smaller pollen than that of macadamia. This caused some difficulty, but was distinguishable because it did not have germ lobes. All of the species with triangular pollen grains could be distinguished from each other by staining with alcoholic iodine-potassium iodide. This solution differentiates macadamia pollen from other triangular pollen by staining starch granules, which occur in a percentage of macadamia pollen, and by distorting the shape of pollen grains other than macadamia.

In table 13 are recorded the percentages of macadamia pollen grains collected at the hives on different dates. The percentages of macadamia pollen became quite high in some hives during the months in which macadamia flowering was at its peak.

Although the number of samples taken was low, it is evident from the data that bees of some hives show a distinct preference for macadamia pollen. This can be explained by the findings of von Frisch (*8*). According to this writer, honeybees can communicate information on (1) direction of a pollen source and approximate distance, (2) strength of nectar, and (3) species from which nectar was derived. Furthermore, Ribbands *et al.* (*20*) have demonstrated that foraging bees develop a hive odor which differentiates bees of different colonies. Ribbands *et al.* further found that, when there is a paucity of nectar, bees from different hives fight one another. These writers stated that the hive odor,

TABLE 13. PERCENTAGE OF MACADAMIA POLLEN AMONG PELLETS COLLECTED AT BEEHIVES OF NUTRIDGE.

COLLECTION DATE	HIVE NUMBER	PELLETS COLLECTED	MACADAMIA POLLEN
		Number	*Percent*
7-27-52	1	61	0.00
8-4-52	2	630	9.36
8-5-52	3	231	8.69
8-8-52	2	579	1.9
10-3-52	4	357	0.56
10-11-52	4	304	1.64
10-20-52	4	1,135	0.52
11-3-52	4	157	0.00
11-20-52	4	302	0.33
12-31-52	4	301	40.53
1-27-53	1	300	1.00
	3	266	9.77
	4	299	52.50
	5	300	0.00
2-5-53	1	150	0.00
	3	150	0.00
	4	150	1.33
	5	150	2.66
2-15-53	1	152	0.00
	3	84	28.57
	4	153	23.52
	5	150	53.33
3-24-53	1	153	13.07
	3	152	51.31
	4	151	48.34
	5	178	17.41
4-29-53	1	164	0.00
	3	150	0.00
	4	153	1.98
	5	152	0.65
5-21-53	1	150	0.00
	3	150	0.00
	4	150	0.67
	5	149	0.00

which apparently derives from the end-products of the type of nectar being collected, is not inherited and may become changed within a few hours. These conclusions imply that under favorable conditions all bee colonies would probably work macadamia.

Collectors make up a major portion of bee populations. A count was taken of pollen– and nectar-collecting bees as they entered the hives at Nutridge. Pollen-collectors were counted at alternate 10-minute periods and nectar-collectors (non-pollen bearing) were counted during intervening 10-minute periods. The percentage of pollen-bearing bees was 35.2 percent.

TABLE 14. NUMBER OF INCOMING POLLEN- AND NECTAR-COLLECTING BEES AT NUTRIDGE DURING ALTERNATE TEN-MINUTE PERIODS. MAY 18, 1952.

PERIOD	POLLEN-COLLECTING	PERIOD	NECTAR-COLLECTING
Time	*Number*	*Time*	*Number*
9:10– 9:20	185	9:25– 9:35	386
9:36– 9:46	155	9:47– 9:57	311
9:57–10:08	162	10:09–10:19	281
10:20–10:30	155	10:31–10:41	366
10:42–10:52	186	10:53–11:03	157
11:04–11:14	90	11:15–11:25	332
11:30–11:40	108	11:43–11:53	402
12:35–12:45	115	12:46–12:56	345
Total	1,156	Total	2,580

EFFICIENCY OF POLLEN COLLECTORS IN DISLODGING POLLEN GRAINS

When tests were being made of the protandry of several varieties, racemes were allowed to flower, and all unopened flowers were stripped off. When these racemes were examined later, 48 flowers of variety 37-6 were intact after 12 hours and 21 flowers of variety 404 had their pollen clumps intact after 48 hours. These figures, in both instances, represented all of the flowers on the racemes. During periods of rainy weather when bees were inactive, several racemes with undisturbed pollen clumps were found at Nutridge. Some of these had flowers with germinated pollen grains. These results indicate that pollen clumps of macadamia, when undisturbed by insect vectors, will adhere to the style tip and cause self-pollination.

Several racemes of varieties shown to be partially self-sterile were bagged, then exposed to bee activity. A raceme of variety 572 was exposed for 32 minutes, during which time two nectar bees and five pollen-collecting bees visited the flowers. At the end of this period, 129 flowers were stripped of pollen clumps. The flowers were rebagged. When examined 15 days later, they showed no initial set.

Two racemes of variety 274 were exposed for 25 and 20 minutes, respectively. The first was visited by one pollen bee for 8 minutes, during which time it stripped 55 flowers of their pollen grains. The second raceme was visited by two pollen-collecting bees for 3 and 4 minutes, respectively, and they accounted for the pollen clumps of 45 flowers. The first raceme had an initial set of 3 fruits, and the second had an initial set of 15 fruits.

A raceme of variety C-324 was exposed for 3 minutes. Two pollen-collecting and two nectar-collecting bees immediately alighted, and they had to be driven off at the end of this period. Thirty-two pollen clumps were disturbed, and an initial set of 17 fruits was obtained.

In the experiments cited above, the honeybees stripped off the pollen clumps of most of the opened flowers. The initial sets of 15 fruits in variety 274 and 17 fruits in variety C-324 indicate that cross-pollination was probably effected by the visiting honeybees, since the mean initial set of the first was 1.33 fruits per raceme, and that of the second was less than one fruit per raceme.

It may be noted in passing that honeybees most heavily work racemes which have both open flowers and unopened buds. Racemes in which most of the flowers are open are visited frequently. Nectar collectors sometimes visit racemes that have buds in which the styles have extruded through the perianth. Racemes in which the sepals have undergone abscission are almost never visited. This is probably because, in the approximately 48 hours during which the sepals adhere to the style, the nectaries of any given flower would have been worked several times. Furthermore, the lower extremities of the sepals act as a container for nectar.

AIRBORNE POLLEN

During the blooming season at Waipahu, pollen grains were observed on leaves of nonflowering trees. A limited trial was, therefore, made at Nutridge. Vaseline slides were hung from leaves on the windward side of a heavily blooming tree. Under extremely favorable conditions, being placed 10 feet above the ground and 6 feet from the outer branches of the tree, one of these slides had 294 pollen grains or clumps on 642 square millimeters of area during a 24-hour period. This averaged out to one pollen clump or grain per 2.18 square millimeters of surface. The stigmatic surface of macadamia is extremely small. In variety 475 this surface is about 0.04 square millimeter of area per raceme. This would thus result in pollination of about four flowers in 28 hours or eight flowers in 58 hours. If wind-pollination were an important factor, under unfavorable conditions of wind, especially with a comparatively great distance separating the trees, it would be expected that the initial set would be low. Since the prevailing winds at Waipahu orchard are rather constant in direction of flow, it would also be expected that the initial set of wide-spaced, partially self-sterile trees would be low in the upper border rows of the orchard, where there are no macadamia trees on the windward side. No such occurrence was noted. Therefore, though wind pollination may be a factor, it is probable that insects are the main pollen vectors of macadamia.

To determine whether pollen shedding is most intense during the day or the night, vaseline-covered slides were hung on leaves of trees in full bloom. The slides were left on for 11½ hours during the evening of May 25-26, 1952 (7:15 p.m. to 6:45 a.m.) and for 11½ hours on the day of May 26 (6:45 a.m.

TABLE 15. POLLEN CLUMPS COLLECTED IN TWENTY-THREE HOURS* AT TREES IN FULL BLOOM.

STATION	SLIDE HEIGHT	POLLEN CLUMPS	
		Night†	Day‡
	Feet	*Number*	*Number*
1	10	1	27
2	10	2	23
3	7	0	12
4	6	1	9
5	5	0	5
Totals		4	76

* May 25 - 26, 1952.
† 7:15 p.m. to 6:45 a.m. (11½ hours).
‡ 6:45 a.m. to 6:15 p.m. (11½ hours).

to 6:15 p.m.). Sunrise on this day was at 5:45 and sunset at 7:07. Thus, the night slides actually were exposed to insect-dislodged pollen clumps for a full daylight hour.

These data indicate either that macadamia does not bloom at night or that insect vectors are relatively inactive at night. The observation that flowers having styles with the double bend do not occur in the early morning hours would indicate that both factors may have affected the result.

SUMMARY

The purpose of this work was to study the floral morphology and behavior of macadamia, especially regarding pollination; determine whether commercial varieties are self-fertile or self-sterile; seek suitable pollenizers if self-sterility was found; and determine the role of pollen vectors.

Pollen grains are deposited on the style tip before and during anthesis. The stigmatic surface of macadamia is so small that it is almost invisible to the unaided eye. The pollen clump does not completely cover the tip of the style but leaves an uncovered diamond-shaped area. Pollen germination in many varieties is first seen at 20 to 26 hours after anthesis; whereas, in sucrose-agar, germination begins 1 to 2 hours after sowing. This, therefore, suggests that the stigma becomes receptive at some period after anthesis.

On the other hand, pollen grains from a different variety, placed on marked style tips of an isolated self-incompatible variety and left unbagged, show a highly significant increase in initial set. This indicates that some measure of stickiness is present in either the pollen grain or stigma before the stigma becomes capable of causing pollen germination.

Anthesis in the local population of macadamia occurs mainly during the day. Also, a great difference is observed in the respective quantities of pollen collected on vaseline-coated slides during the night and during the day.

Partial self-incompatibility was found in the majority of local trees of macadamia. However, several varieties were found which appeared to be almost completely self-compatible. Self-compatibility was tested mainly by the initial set. Trees having a modal initial set of zero per raceme were considered to be partially self-incompatible. In all cases tested, the initial set of partially self-incompatible varieties could be raised to much higher levels by cross-pollination. However, the high initial sets of macadamia undergo a rapid fall during the first month after anthesis.

The four commercial varieties tested at Waipahu were all found to be mutually cross-compatible. Varieties 246, 425, and 508 have peak blooming periods that almost coincide. Variety 336 has a peak blooming period which occurs somewhat later. All four varieties show considerable overlap in blooming periods.

In two orchards which were studied, the predominant pollen vectors of macadamia were insects. Wind pollination could not be wholly discounted, however, because enormous amounts of pollen are discharged by the flowers.

The pollen-collecting honeybee is the most active insect on macadamia flowers. It is also the only insect that comes into regular contact with the stigmatic areas of the style. This contact occurs because macadamia flowers, in common with those of other proteads, deposit their pollen grains on the style tip. The other insects which occur most frequently on macadamia flowers in-

clude the syrphid flies and the nectar-collecting honeybee. They work the flowers at the level of the nectaries, which occur at the base of the style. Since they are often found covered with pollen grains, some cross-pollination is probably effected by the nectar feeders.

Pollen pellets were stripped from the corbicula of the honeybee, at the hive, by means of a Kremer trap. They were found to have relatively high percentages of macadamia pollen.

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UNIVERSITY OF HAWAII
COLLEGE OF AGRICULTURE
HAWAII AGRICULTURAL EXPERIMENT STATION
HONOLULU, HAWAII
